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Are all edges equal? Microclimatic conditions, geographical orientation and biological implications in a fragmented forest

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ABSTRACT

In fragmented forests the edges experience changes in microclimatic conditions, which are referred to as "abiotic edge effect", and differ according to geographical orientation and season. These microclimatic changes could influence the development rate of the organisms (particularly for movement - restricted ones like leaf miner larvae and their parasitoids) and, consequently, their population dynamics. The aim of this study was to compare the abiotic edge effect in differently oriented edges in summer and winter seasons, and evaluate possible implications on insect development, using a simulation based on a degree-day approach. To compare the abiotic edge effect, we took continuous and point measurements of microclimatic variables such as temperature, humidity, wind velocity and interception of photosynthetically active radiation in three microhabitats: interior (I), north-facing edges (NE) and south-facing edges (SE) of six fragments of Chaco Serrano forest, in winter and summer seasons. As we expected, the microclimatic edge effect was greater in NE compared to SE in both seasons. In winter, the differences were more pronounced only for continuous measurements of temperature. Our simulation exercise suggested that differences in temperature among microhabitats may have biological implications on insect populations, affecting their development time. At larger scales, an increase of temperature could lead to more frequent pest outbreaks which could extend their distribution range to higher latitudes. Our findings emphasize the need to consider geographical orientation and season variations when studying edge effects on insect populations. In the context of climate change, organisms could restrict their distributions to habitats with more suitable conditions, becoming microrefuges that could allow them to survive. Moreover, in fragmented landscapes, identifying microhabitats benefitting or harming insect populations is an important step to design management strategies towards pest control or natural enemy conservation in agricultural settings.

1. Introduction

In fragmented forests, the ecological conditions of the edges contrast with those of the interior with regard to the structural complexity of vegetation and biomass, which in turn generates differences in microclimatic conditions (Davies-Colley et al., 2000; Murcia, 1995). The changes in microclimatic conditions that occur at the edges and that result from the edge proximity to a structurally dissimilar matrix, are termed "abiotic (or microclimatic) edge effect" (Magura, 2017; Murcia, 1995; Norton, 2002). There is considerable evidence that forest edges experience higher radiation levels, more elevated and more variable air and soil temperatures, stronger winds and lower moisture levels than forest interiors (Chen et al., 1995; Denyer et al., 2006; Matlack, 1993; Norton, 2002). Such microenvironmental conditions could dramatically alter the composition and distribution of organisms and the biological processes in which they are involved (Chen et al., 1993; Harper et al., 2005; Wirth et al., 2008). Insects in particular, being ectothermic organisms with biochemical and physiological processes dependent on ambient temperature, are strongly influenced by thermal variations (Deutsch et al., 2008; Robinet and Roques, 2010). Increasing temperatures can accelerate development rates and the number of generation of insects per year (Abram et al., 2017; Bale et al., 2002; Buckley et al., 2017; Forrest, 2016), as long as these temperatures remain within favored ranges for the species (Trudgill et al., 2005).

Some studies showed that ectothermic organisms living in the tropics are more vulnerable to elevated mean temperatures than those in temperate areas (Abram et al., 2017; Deutsch et al., 2008; Thomas et al., 2012). Climate change scenarios predict an increase in the

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magnitude and frequency of extreme temperatures that could overtake organism thermal thresholds for growth and reproduction, reducing their development rate, fecundity, and survival (CaraDonna et al., 2018; Sentis et al., 2017; Sinclair et al., 2016). Furthermore, climatic variability could cause a mismatch between the phenology of organisms within a food chain due to a differential response of species across trophic levels (Bannerman et al., 2011; Both et al., 2009; Pureswaran et al., 2015; Van Asch et al., 2007). Therefore, changes in temperature such as those that may occur at forest edges could affect insect development and consequently, influence their population dynamics in fragmented landscapes (Hance et al., 2007; Thomas and Blanford, 2003).

The abiotic edge effect may be influenced by geographical orientation, which determines differences in the amount of exposure to solar radiation (Chen et al., 1995; Gehlhausen et al., 2000; Heithecker and Halpern, 2007; Murcia, 1995). This in turn generates differences in heat load and moisture levels (Arroyo-Rodriguez et al., 2017; Matlack, 1993). Edges facing the poles receive less radiation compared to edges facing the equator; therefore, microclimatic conditions at the former tend to be more stable, with weaker abiotic edge effects (Burton, 2002; Harper et al., 2005; Landenberger and Ostergren, 2002; Matlack, 1993; Murcia, 1995). Thus, studies conducted in the Northern Hemisphere found that south-facing forest edges had the highest peaks of daily temperature (Chen et al., 1993). By contrast, in the Southern Hemisphere, north-facing forest edges showed higher temperatures, stronger winds and lower humidity than south-facing edges (Norton, 2002).

The microclimatic edge effects in edges with different geographical orientations could change seasonally (Davies-Colley et al., 2000; Denyer et al., 2006; Didham and Lawton, 1999; Young and Mitchell, 1994). In summer months, the sun is higher in the sky, reducing the shadow effect between differently oriented edges (Kumar et al., 1997). In winter, on the other hand, the light incidence angle is lower; therefore, microclimatic differences will greatly depend on edge orientation (Dobrowski et al., 2009).

Few studies have investigated microclimatic conditions of differently oriented forest edges (Chen et al., 1993, 1995; Gehlhausen et al., 2000; Heithecker and Halpern, 2007; Matlack, 1993; Norton, 2002; Young and Mitchell, 1994) and even fewer have examined changes across seasons (Young and Mitchell, 1994). At local level, assessment of microhabitat suitability can be used as a method of approximation to understand and predict species response to global climate change at higher spatial scales (Barton et al., 2018; Bennie et al., 2008; Gillingham et al., 2012; Herrera et al., 2014).

Chaco Serrano is a seasonally dry subtropical forest from Central Argentina which in recent years lost over 90% of its original cover due to the advance of agriculture, and it is now a fragmented landscape restricted to remnants of different sizes (Zak et al., 2004). The aim of this study was to compare the microclimatic edge effect between north and south-facing edges, in Chaco Serrano forest fragments. We expected microclimatic edge effects to be greater in north-facing edges than in south-facing edges, and the differences to be more pronounced in winter than in summer. In addition, we evaluated the biological implications of these microclimatic variations on the development time of a phytophagous leaf miner and three of its parasitoid species, by performing a simulation exercise based on their thermal requirements.

The leafminer species modeled in this study, *Liriomyza huidobrensis* (Blanchard) (Diptera: Agromyzidae), is a worldwide pest native to South America and first described from Argentina, which causes economic losses on a variety of horticultural and ornamental crops (Weintraub et al., 2017). At the study region, the leaf miner attacks both native and cultivated hosts (Valladares, 1984; Valladares and Salvo, 1999), being more abundant in urban and cultivated habitats than in natural environments such as Chaco forest, where it is nonetheless present. The forest fragments in which our study was performed are important reservoirs of many parasitoid species frequently associated to this leaf miner (Salvo et al., 2005; Cagnolo et al., 2011). Biological control is considered an effective management strategy for this pest, given the large diversity of parasitoids attacking *L. huidobrensis* worldwide (Weintraub et al., 2017). Such biological control could be enhanced by the intense movement of natural enemies from remnants of Chaco forest to adjacent crops, reported for this area (González et al., 2016).

Degree-day models have been developed to characterize the relationship between temperature and ectotherm development rates, and are often used in an attempt to predict organisms responses to climate change (Rebaudo and Rabhi, 2018; Sinclair et al., 2016). We predict development to be slower in north-facing edges compared to south-facing edges in summer, because temperature values in the north edges would exceed the upper development thresholds for the species more frequently than in the south edges. We predict the opposite trend in winter. Finally, we expected differences in development speed between the edges to be more marked in winter than in summer.

2. Materials and methods

2.1. Study region and sites selection

The study was conducted in a semi-arid Chaco Serrano area (31° 09′S–31° 13′S and 64° 13′W–64° 17′W) in Córdoba, central Argentina. This region has an elevation of between 500 and 1300 m.a.s.l, with an average annual rainfall of 750 mm concentrated mainly in the warm season (October–April), and average maximum and minimum temperatures of 26 °C and 10 °C respectively (Luti et al., 1979). Native vegetation is characterized by an arboreal stratum (8–15 m) dominated by *Aspidosperma quebracho-blanco* Schltdl., *Prosopis* spp., *Fagara coco* Engl. and *Lithraea molleoides* (Vell.); a shrub layer (1,5–3 m) with *Celtis ehrenbergiana* (Klotzsch) Liebm. and *Acacia* spp.There are also herbs and grasses (0–1 m) and several vine species (Luti et al., 1979). Currently, this area is restricted to forest remnants of variable sizes within a predominantly agricultural matrix (Zak et al., 2004). Through digital satellite images (Landsat TM) and field observations, we selected six forest remnants of 10–20 ha each, hereafter “sites” (replicates), separated from each other by a distance of about 300 m. In summer of 2013 and 2014, sites were surrounded by a soybean and maize matrix, respectively, whereas in winter of 2014, the matrix consisted of bare soil. In each site, we delimited three forest microhabitats “locations”: interior (“I”) located 30–35 m from the dividing line matrix-forest, a north edge (“NE”) and a south edge (“SE”) located 2 m from the dividing line matrix-forest and geographically oriented towards the north and south, respectively.

2.2. Microclimatic conditions measurements

During March of 2013 and January, March and August of 2014, we measured air temperature, humidity, wind speed and photosynthetically active radiation (PAR) under the canopy in each location (I, NE and SE) of the six sites. Air temperature, relative humidity and wind speed–direction, were assessed by means of a weather station TFA “SINUS” 31.1095 placed 1 m above ground level (AGL), whilst photosynthetically active radiation (PAR) values were recorded through a ceptometer LICOR (LI-COR Environmental, Lincoln, NE, USA) (Stoutjesdijk and Barkman, 1992). These point measurements were obtained with a maximum difference of 90 min in the three locations of each site, during the period of highest solar radiation (12–13:30 h), when the temperature and moisture tend to be more stable in comparison to other moments of the day (Davies-Colley et al., 2000; Denyer et al., 2006). In order to minimize variations due to the time of data registration, location measurements were taken in random order on each site. The weather station recorded measurements every 5 min during 20 min (n = 4) in each location. Simultaneously, 10 measurements of PAR were recorded under the canopy separated from each other by 5 m, in a 50 m transect. At the same time, we measured PAR

values in places without canopy to determine the percentage of interception of photosynthetically active radiation (IPAR). These values indicate the proportion of available solar radiation that does not reach the microhabitat. Point measurements were recorded in each site on different days.

Continuous records of air temperature were also taken through data-loggers (iButton DS- 1921G-F5) that registered measurements every hour during 7 days, twice during summer (January 2013 and February 2014) and once during winter (August 2014). In 2013, we wrapped data-loggers in plastic bags covered with burlap bags that functioned as camouflage to avoid vandalism, and we suspended them on trunk trees at a 1 m height. To avoid a potential increment in humidity due to the plastic bags, in 2014 we settled data-loggers in plastic containers opened downwards with lateral perforations to allow air flow. However, both methodologies yielded statistically similar results suggesting that plastic bags did not increase humidity. We used continuous measurements to calculate daily temperature range, mean daily temperature and temperature by time zones (TZs): 0–5 h (TZ1), 6–11 h (TZ2), 12–17 h (TZ3) and 18–23 h (TZ4).

Measurements of temperature and humidity at soil level were incorporated in winter, since pupal stages of the insects addressed in this study tend to spend cold seasons in the surface litter, attached to the fallen leaves (Carballo et al., 1990). In the case of point measurements, we used the data of temperature and humidity registered by the console of the weather station placed at ground level. Data-loggers measuring continuous data of air temperature were protected by plastic containers located at the base of trees, a few centimeters above ground level, to enable air flow. In winter, IPAR measurements were obtained with a different methodology, given operating problems with the ceptometer. In each location, we took 10 photos separated from each other by 5 m, from a 1 m height and pointing the objective upwards, with a photographic camera Canon PS SX30. These photos were processed using the ImageJ software (Rasband, 1997–2012Rasband, 1997Rasband, 1997–2012), which allows to separate the image into green (vegetation) and non-green (sky) areas, by adjusting hue (between 0–150), saturation (between 0–80) and brightness (between 30–80) threshold settings to match the observed green. The area of the green portion in the picture was taken as estimation of the IPAR.

2.3. Degree-day summation approach

We performed a simulation exercise to assess the effect of microclimatic thermal variations on insect development. We chose four model species for this study on the basis of their worldwide relevance and availability of information about their developmental thresholds: *Liriomyza huidobrensis*, an important leaf miner pest of various vegetable crops worldwide (Weintraub et al., 2017), and three of its associated parasitoids, namely *Phaedrotoma scabriventris* (Hymenoptera: Braconidae), *Chrysocharis vonones* and *Chrysocharis flacilla* (both Hymenoptera: Eulophidae) (Costa-Lima et al., 2014; Fenoglio and Salvo, 2009; Mujica et al., 2016; Salvo et al., 2005). This leaf miner is found at low densities in the studied fragments, whereas its generalist parasitoids are very abundant (Cagnolo et al., 2011). Since insect development is a temperature-dependent process, we simulated it following a degree-day summation approach as an expression of thermal time. This method is usually applied to predict insect phenology, the sequence of either life stages or generations, by calculating the proportion of a given stage that is attained daily or in a given period of time. The thermal constant (K) is the number of degree-days needed to complete the developmental process (Trudgill et al., 2005). The lower development threshold (°C) is the minimum temperature at which development occurs, while an upper threshold is considered to take into account that temperatures too high may cause complete interruption or sharp decrease of development rate.

For each species, we calculated the degree-days achieved each day in hourly time steps using the following formula:

$$D(h) = \frac{MIN(T_U,\ T) - MAX(T_L,\ T)}{24} \quad (1)$$

$$DD = \sum_{h=1}^{h=24} D(h) \quad (2)$$

where D(h) is the degree days accumulated during the hour h, T is temperature recorded at hour h, T_L and T_U are the lower and upper development threshold, respectively. MIN and MAX are operations selecting the minimum and maximum elements of the argument. Eq. (1) is divided by 24 in order to be used at an hourly time step. For each day, the degree days (DD) are calculated with Eq. (2). Then, DDs were summed over the period of continuous air temperature recordings. For each species, the accumulated degree-days were divided by K, yielding the proportion of the whole cycle that would be attained during the sampling period of continuous measurements of temperature: two weeks in summer and one week in winter, in the three locations (NE, I, SE). For each of the four model species, the egg-to-adult thermal constant K and the T_L and T_U parameters were taken from the literature (Costa-Lima et al., 2014; Lanzoni et al., 2002; Mujica et al., 2016).

2.4. Statistical analysis

Summer and winter data, as well as data of measurements taken at different levels (1 m AGL and soil level) in winter were separately analyzed. We employed linear mixed effects models (LMM) (Zuur et al., 2009) to compare point measurements of microclimatic variables among locations (fixed effect) with sampling date nested into site as random effects in case of summer data. In the case of continuous measurements, we performed similar models for continuous measurements but we incorporated the day nested into the sampling date and nested into the site as random effects for summer and winter data, respectively. To correct residual variance heterogeneity between microhabitats of wind velocity data, VarIdent function (form = ~1|microhabitat) was used (Zuur et al., 2009). We applied Principal Components Analyses (PCA) to study the relationship between the microclimatic variables obtained in each location (NE, I, SE) of each site of Chaco forest. Previously, the multicollinearity between microclimatic variables was explored, and only one variable from a pair highly correlated (Pearson Coefficients higher or equal to 0.7) was included in the models. We also evaluated the proportion of complete life cycle attained by each species under each thermal conditions in the simulation exercise, using linear mixed effects models, with location, species and the interaction between them as fixed factors and site and sampling date (summer data) or just site (winter data) as random effects. When the interaction was not significant, we removed the term from the model. The data were analyzed with R software version 3.3.1 (R Development Core Team, 2016).

3. Results

3.1. Microclimatic conditions and abiotic edge effect

Throughout the summer season, point temperature (T_p) was significantly higher in north-facing edges (NE) compared to the forest interior (I) and south-facing edges (SE), where T_p did not differ (Fig. 1a, Table 1). However, during winter, we did not find significant differences of T_p between locations at both 1 m AGL and soil level (Table 1, Fig. 1a). Regarding mean temperature (T_m) recorded by data-loggers, we observed significant differences between microhabitats in summer season (Table 1). T_m was lower in the interior than in the edges, and there were no differences between the edges with different geographic orientation (Fig. 1b). In winter, however, T_m was higher in NE, followed by I and finally by SE, location with the lowest mean temperature values at both 1 m AGL and soil level (Table 1, Fig. 1b). The differences between the edges were almost three times greater at soil level.

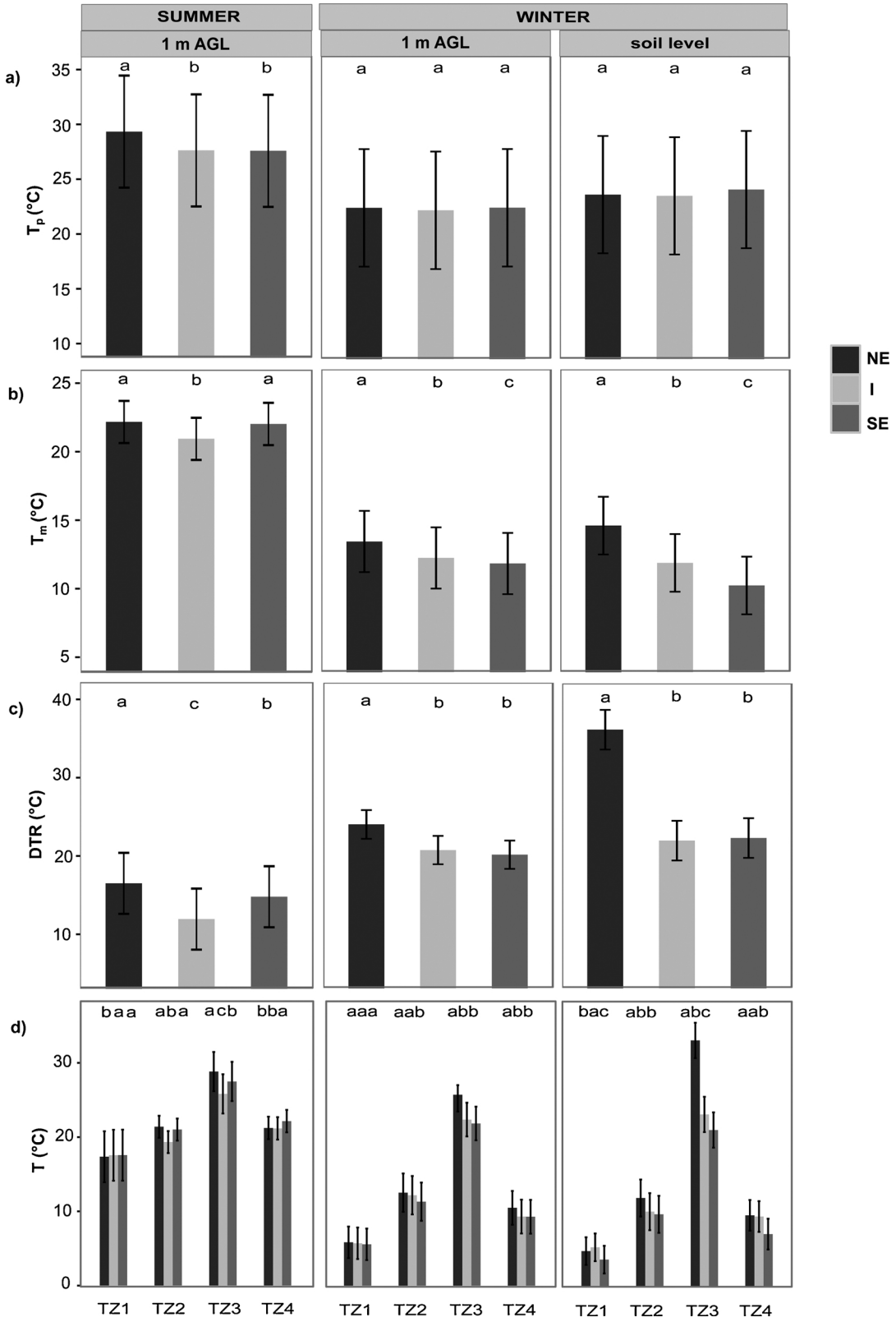

Fig. 1. Comparisons of a) point temperature (T_p), b) mean temperature (T_m), c) daily temperature range (DTR) and d) temperature by time zone (T) among locations: forest interior (I), and north and south-facing edges (NE, SE), during summer and winter season, at both 1 m AGL and soil level. The averages of the six sites are shown. Bars represent 95% confidence intervals from the linear mixed effect models (LMM). Different letters show significant differences ($p \leq 0.05$) among locations.

Additionally, daily temperature range (DTR) differed significantly between locations in summer and winter, both at 1 m AGL and soil level (Table 1). In summer, DTR was higher in NE with respect to SE and I, the latter being the most stable microhabitat regarding thermal values (Fig. 1c). In winter, temperature fluctuations were greater in NE in comparison to SE and I, at both 1 m AGL and soil level (Fig. 1c). Differences in DTR between the edges were more than two times greater in winter than in summer, and during the cold season, the differences

Table 1
Results of linear mixed effects models (LMM) comparing microclimatic variables among locations, in both summer and winter seasons, at 1 m AGL and soil level. Abbreviations: point temperature (T_p), mean temperature (T_m), daily temperature range (DTR), temperature (T) by time zone (TZ), relative humidity (H_r), wind velocity (V) and interception of photosynthetically active radiation (IPAR).

Season	Microclimatic variables	Df	F	P
Summer	T_p	2,34	6.79	0.003
	T_m	2,166	88.20	< 0.0001
	DTR	2,166	34.86	< 0.0001
	T_{TZ1}	2,166	2.9	0.05
	T_{TZ2}	2,166	50.13	< 0.0001
	T_{TZ4}	2,166	51.4	< 0.0001
	H_r	2,34	9.04	< 0.0001
	V	2,34	26.21	< 0.0001
	IPAR	2,22	4.35	0.026
Winter	T_p	2,10	0.05	0.95
	T_p (soil level)	2,10	0.14	0.87
	T_m	2,94	1.08	< 0.0001
	T_m (soil level)	2,94	237.06	< 0.0001
	DTR	2,94	27.83	< 0.0001
	DTR (soil level)	2,94	128.87	< 0.0001
	T_{TZ1}	2,82	0.66	0.52
	T_{TZ1} (soil level)	2,82	20.21	< 0.0001
	T_{TZ2}	2,88	8.09	0.0006
	T_{TZ2} (soil level)	2,88	23.73	< 0.0001
	T_{TZ3}	2,88	97.14	< 0.0001
	T_{TZ3} (soil level)	2,88	215.62	< 0.0001
	T_{TZ4}	2,82	23.77	< 0.0001
	T_{TZ4} (soil level)	2,82	77.79	< 0.0001
	H_r	2,10	0.21	0.82
	H_r (soil level)	2,10	0.85	0.46
	V	2,10	1.86	0.21
	IPAR	2,10	18.53	< 0.0001

were more pronounced (more than three times) at soil level (Fig. 1c).

When we discriminated temperature (T) by time zone (TZ), we observed that the differences between locations depended on day time and season (Table 1). Temperatures measured between 12–17 h (TZ3) were the highest in both seasons. In summer, the temperature in TZ3 was greater in NE, followed by SE and finally by forest interior (Fig. 1d). In winter, the highest temperature values of TZ3 were also recorded in NE, but in this season, SE and I showed similar values (Fig. 1d). At soil level, the temperature in TZ3 was higher in NE compared to the forest interior and SE, the latter being the coolest microhabitat (Fig. 1d). The differences in temperature of TZ3 between the edges were almost 3 times greater in winter season in comparison to those recorded in summer, particularly at soil level, where differences were even more pronounced.

We found significant differences in relative humidity (H_r) between locations in summer season (Table 1). The lowest moisture levels were observed in NE, the forest interior exhibited the highest, and SE showed intermediate values (Fig. 2a). However, the percentage of humidity did not differ between locations in winter season at both 1 m AGL and soil level (Table 1, Fig. 2a). In summer, wind velocity (V) was higher in NE followed by SE and finally by I (Table 1, Fig. 2b), but we did not observe differences in wind speed in winter (Table 1, Fig. 2b). Finally, in summer season, IPAR was higher in the forest interior and in SE with respect to NE (Table 1, Fig. 2c), whereas in winter, the forest interior showed the highest percentage of IPAR, and there were no differences between the edges with different orientation (Table1, Fig. 2c).

The PCA showed a clear separation of microhabitats in summer season (Fig. 3a), in which the first two components of PCA accounted for 63% of the total variance. North-facing edges were associated with greater values of wind velocity and more fluctuating and higher temperatures in TZ4 (18–23 h). Forest interiors occupied the opposite side in the ordination plane, and were associated to lower values of temperature and wind velocity, higher moisture levels and greater IPAR, whereas south-facing edges occupied an intermediate position between the other microhabitats. Similar but less marked patterns were observed in PCA ordinations of winter season data taken at both 1 m AGL and soil level (Fig. 3b–c), in which the first two axis accumulated 69.93% and 79.70% of the total variance, respectively. In both cases an obvious separation between NE and I was observed, with SE and I points mostly overlapped. At 1 m AGL, NE were characterized by higher daily temperature ranges, greater values of temperature in TZ2 (6–11 h) and TZ4, and stronger winds. At soil level, NE were associated with greater DTR and higher temperatures in TZ2 and TZ4.

3.2. Thermal time simulation exercise

In summer, according to our simulations, life cycles of *L. huidobrensis* and its associated parasitoids (*P. scabriventris*, *C. vonones* and *C. flacilla*) would be completed faster in the edges than in the forest interior, with no differences between the edges (Table 2, Fig. 4). Also, species development would follow a decreasing gradient of speed from *C. vonones, P. scabriventris*, *L. huidobrensis* to *C. flacilla,* without differences between the last two species (Table 2, Fig. 4). In winter, the leaf miner *L. huidobrensis* and its associated parasitoids would develop faster in NE, followed by the interior and finally by SE (Table 2, Fig. 4). Similarly, in winter the leaf miner showed the slowest development speed and *C. vonones and P. scabriventris* the fastest (Table 2, Fig. 4).

4. Discussion

4.1. Abiotic edge effects and biological implications in relation to edge orientation and season

Our results showed a clear differentiation of microclimatic conditions among microhabitats in both seasons. During summer, the edges experienced more elevated and fluctuating temperatures, lower moisture levels and stronger winds than the forest interior, whereas higher insolation was observed in north-facing edges. These findings are consistent with available evidence about changes in microclimatic conditions due to edge effect in fragmented forests (Chen et al., 1993;Davies-Colley et al., 2000 Denyer et al., 2006; Heithecker and Halpern, 2007; Matlack, 1993; Norton, 2002; Young and Mitchell, 1994). In addition, interesting daily temperature variations were observed. During most of the day (6–17 h), the temperature inside the forest was colder than that of both edges, while at night, I and SE were warmer than NE. Higher levels of re-emission of energy (the one absorbed by canopy during day and released at night) in I and SE compared to those at NE, could explain the variations in observed temperature (Wright et al., 2010).

Moreover, our results revealed a strong influence of geographical orientation on edge microclimatic conditions, also highlighting the importance of including a large number of microclimatic variables in the analyses. In summer, NE exhibited higher temperatures in the warmer hours (from 12 to17 h) and point temperature, greater daily temperature ranges, higher solar radiation, stronger winds, as well as lower humidity levels compared to SE. These findings were consistent with our predictions and results of previous works exploring the effects of geographical orientation on microclimatic edge effect in forest areas (Chen et al., 1993, 1995; Gehlhausen et al., 2000; Heithecker and Halpern, 2007; Matlack, 1993; Norton, 2002; Young and Mitchell, 1994). These variations were attributed mainly to the solar angle that is higher in edges facing the equator than in those facing the poles (Murcia, 1995). Consequently, in the southern hemisphere, north-facing edges receive greater direct solar radiation than do south-facing edges and, therefore, experience higher temperature levels and lower humidity (Cadenasso et al., 1997; Matlack, 1993; Murcia, 1995; Norton, 2002). Besides solar radiation, changes in wind speed and direction between differently oriented edges may contribute to enhancing differences in other microclimatic variables as temperature and humidity

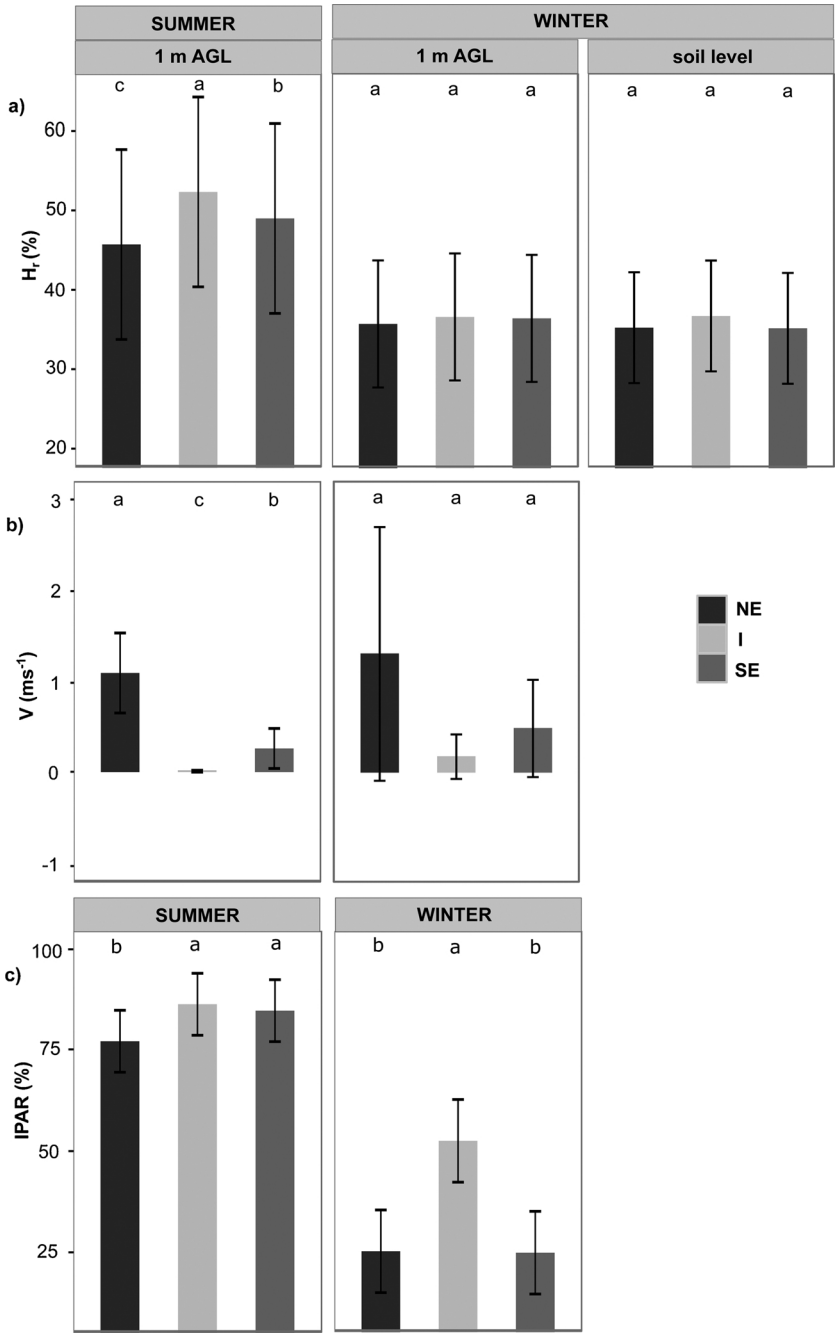

Fig. 2. Comparisons of a) relative humidity (H_r), b) wind velocity (V) and c) interception of photosynthetically active radiation (IPAR) among locations: forest interior (I) and north and south-facing edges (NE, SE) during summer and winter season, at both 1 m AGL and soil level (in case of H_r). The averages of the six sites are shown. Bars represent confidence intervals (± 95%) from the linear mixed effect models (LMM). Different letters show significant differences ($p \leq 0.05$) among locations.

(Davies-Colley et al., 2000). In the study site, prevailing winds come from the northeast sector, which helps to increase the differences between the edges.

However, in summer, the mean temperature did not vary between edges with different orientation. According to Matlak (1993) and Kumar et al. (1997), thermal differences between orientations decline in summer because the sun hits the earth more perpendicularly, thus reducing shadow effect in southern orientations. This also applies for higher latitudes with respect to equator, at a regional scale (Kumar et al., 1997). Additionally, differences in temperature were more pronounced in the early afternoon, which agrees with previous studies (Denyer et al., 2006).

In winter, all locations experienced similar point temperature and humidity both at 1 m AGL and soil level, and comparable wind velocity. Similarly, differences between the forest interior and the edges in winter months have not been observed in temperate forests of New Zealand (Young and Mitchell, 1994).The lower sun angle in winter season could lead to enhancing the differences in microclimatic conditions between orientations (Dobrowski et al., 2009; Kumar et al., 1997), however, in our study, these differences were less obvious regarding point measurements. Prevailing northeastern winds in winter could be replaced by more frequent cold southern winds, masking differences between the edges.

However, continuous temperature measurements registered by

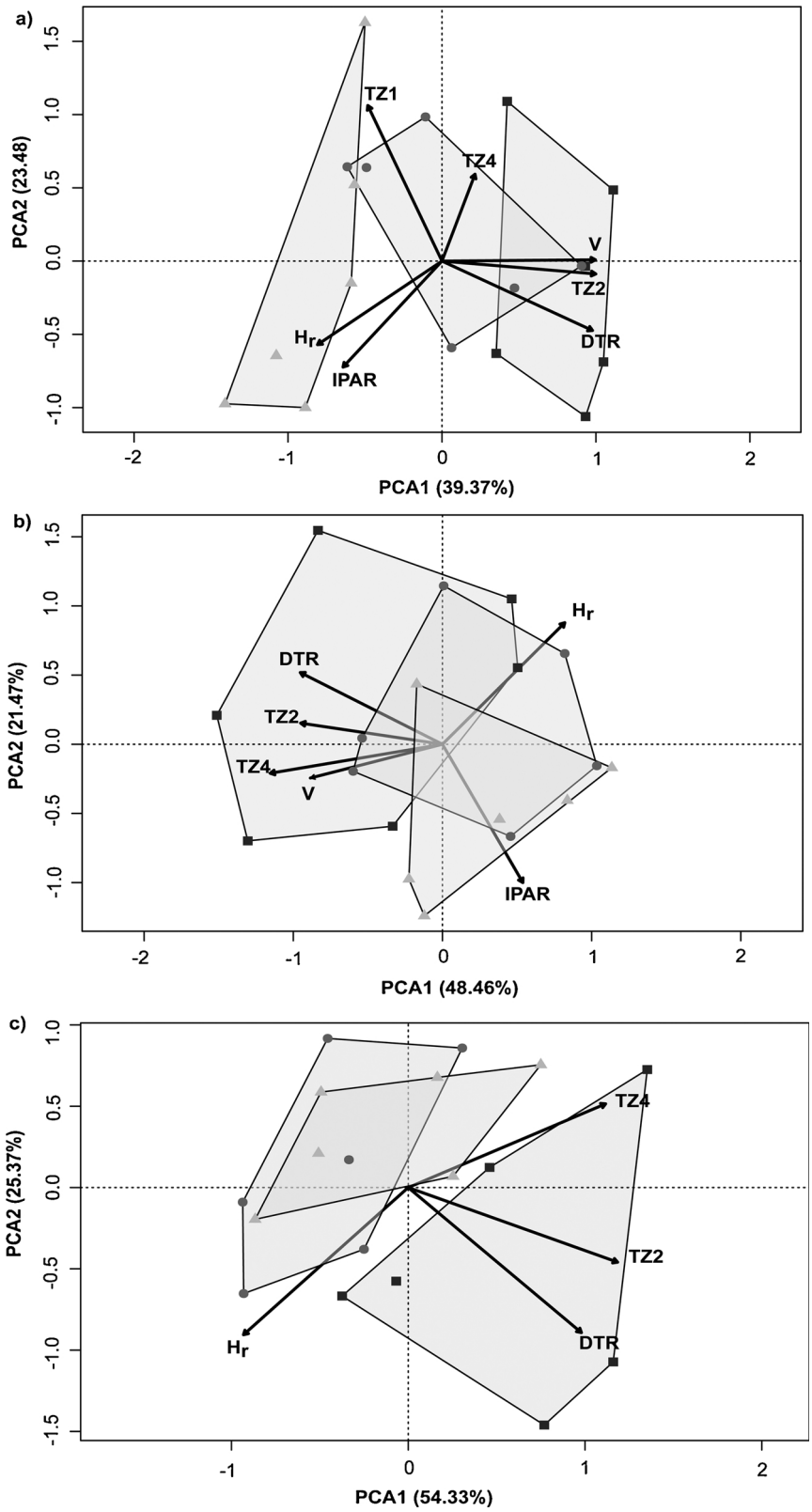

Fig. 3. Principal component analysis (PCA) biplot of microclimatic variables in forest interior (triangles), and north (squares) and south-facing edges (circles) in a) summer at 1 m AGL, b) winter, 1 m AGL and c) winter, soil level. Abbreviations: daily temperature range (DTR), temperature between 0–5 h (TZ1), temperature between 6–11 h (TZ2), temperature between 18–23 h (TZ4), relative humidity (H_r), wind velocity (V) and interception of photosynthetically active radiation (IPAR).

data-loggers at both 1 m AGL and soil level, showed a different pattern of variation. We found significant differences in mean temperature, daily temperature range and temperature (mainly from 12 to 17 h) between different edge orientations. This highlights the better assessment of continuous measurements providing large amounts of data. In this case, as we expected, differences were even more pronounced in winter than in summer. Besides, differences in these continuous variables were even more evident at soil level. These results

Table 2
Results of linear mixed effects models (LMM) comparing the proportion of life cycles completed in a fixed time period by the leaf miner *Liriomyza huidobrensis* and three associated parasitoids (*Phaedrotoma scabriventris*, *Chrysocharis vonones* and *Chrysocharis flacilla*) among locations, in both summer and winter seasons.

Season	Explanatory variables	Df	F	P
Summer	Location	2,127	95.00	< **0.0001**
	Species	3,127	454.36	< **0.0001**
Winter	Location	2,61	160.02	< **0.0001**
	Species	3,61	33.40	< **0.0001**

were consistent with those found by Chen et al. (1993) in forest located in southern Washington (USA) and could be related to the moderating effect exercised by the wind that mixes the air, thus reducing temperature variations.

The results found in this study have implications for conservation strategies. Several studies recommended the creation of a forest buffer adjoining borders and open areas to reduce the magnitude of edge effect (Davies-Colley et al., 2000; Denyer et al., 2006). In the southern hemisphere, north-facing edges should be considered as the primary candidates for protection. Buffers could mitigate the effects of thermal variation, stronger winds and water stress of NE on living organisms.

Results of the simulation exercise suggested that the observed differences in temperature among locations may have biological implications on demographic aspects of insect populations. Thermal variations could be inducing changes in the phenology dynamics of insect populations, with different outcomes in summer and winter, as observed for *Liriomyza huidobrensis* and three of its parasitoid species. In summer, the leaf miner as well as all three associated parasitoid species would complete their life cycle faster in either edge than in the forest interior. Therefore, our simulations suggest that higher mean temperatures and greater thermal variations in the edges, rather than limiting insect development due to exceeding upper thresholds for the species, would accelerate it. Temperature values at the edges were, with few exceptions, within the optimal thermal thresholds for these species, thus higher temperatures would result in faster development (Deutsch et al., 2008; Frazier et al., 2006; Huey and Stevenson, 1979). Temperatures above the upper thermal threshold for these species may have not been frequent or prolonged enough to alter negatively their development speed. Moreover, ectothermic organisms have the capacity to change their physiology and behavior to tolerate and adapt to their thermal environment (Abram et al., 2017). In the hottest hours, insects could take refuge at fresher shady places or could move to the forest interior to cope with maximum extreme temperatures of the edges, although such possibility does not apply to the studied larvae, which are restricted to the interior of individual leaves. However, the oviposition behavior of the adult female could also affect larval performance (Bonebrake et al., 2010; Grossmueller and Lederhouse, 1985; Williams, 1981). For example, females could lay their eggs in shaded places to protect the offspring from extreme temperatures.

In winter, more benign temperatures in north-facing edges might have led to faster development with respect to south-facing edges and forest interior, where low temperatures could delay the beginning of the activity of the studied species, prolonging their development time or diapausal stage. Bonebrake et al. (2010) found that in the coldest years, when thermal constraints on development time are stronger, females of the butterfly *Euphydryas gillettii* selected oviposition sites in more open habitats and laid their egg clusters more frequently intercepting the morning sun, to increase larval survival. As we expected, predicted differences in development speed of the studied species between differently oriented edges were more pronounced in winter, in coincidence with greater differences in mean temperatures.

These results may have implications at a regional scale, since temperature increments could enhance *L. huidobrensis* fitness, allowing its range expansion to more southern regions and higher altitudes globally (Weintraub et al., 2017). Furthermore, the leaf miner will develop more generations per year, increasing their abundance and the frequency of possible outbreaks. Moreover, temperature differences between edges at higher latitudes could promote habitat heterogeneity, allowing species to take refuge in suitable microhabitats in order to cope with global warming. This could be less feasible at lower latitudes where microclimatic differences among edges would be minimal.

Parasitoids attacking *L. huidobrensis* also increased their performance at higher temperatures. In our study system, forest fragments can act as reservoirs of these natural enemies (Rossetti et al., 2013). Also, in the same region, natural enemies have been shown to move frequently to adjacent crops (Gonzalez et al. 2016), and the presence of forest in the landscape has been linked to improved pest control (González et al. (2017)). Therefore, in the case of *L. huidobrensis*, farmers may enhance biological control and thus mitigate crop damage by this leaf miner pest by conserving forest fragments in the agricultural landscape, particularly those with a greater extent of north-facing edges. An important point to consider in relation to this simulation is the possible asynchrony among life cycles of interacting species within food chains, as a result of differential vulnerability to thermal variations (Bannerman et al., 2011; Pureswaran et al., 2015; Sinclair et al., 2016). For example, the faster development of *C. vonones* and *P. scabriventris* could lead to a phenological mismatch between them and their host, *L. huidobrensis*, which is expected to show a weaker acceleration. The emergence of parasitoids during a temporal window of host unavailability in the habitat could lead to a reduction of parasitoid fitness and, consequently, of biological control effectiveness.

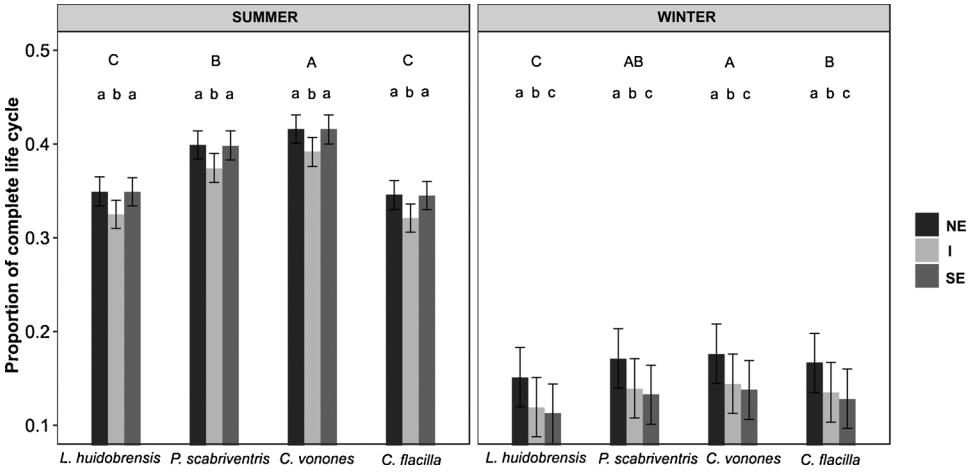

Fig. 4. Comparisons of the proportion of complete life cycles of the leaf miner *Liriomyza huidobrensis* and three of its associated parasitoids (*Phaedrotoma scabriventris*, *Chrysocharis vonones* and *Chrysocharis flacilla*) among locations: forest interior (I), and north and south-facing edges (NE, SE) during summer and winter season. The averages of the six sites are shown. Bars represent confidence intervals (± 95%) from the linear mixed effect models (LMM). Different lowercase and uppercase letters show significant differences ($p \leq 0.05$) among locations and species, respectively.

Caution is needed to interpret results from degree-day models. Firstly, they used to be built using insect exposure to constant temperatures; therefore, extrapolating these models to field conditions can be complicated in heterogeneous environments (Sinclair et al., 2016). In addition, one of the main limitations of degree-day models is that they do not consider mortality at extreme temperatures (Rebaudo and Rabhi, 2018). The simulation here performed was based on actual microclimatic data, but still overlooking the possibility of insect death at lethal temperatures. Despite its limitations, the degree-day model is the most popular phenological model for predictions about insect development in the context of climate change, although other approaches (e.g. thermal performance curve with fluctuating temperatures) could be incorporated (Rebaudo and Rabhi, 2018).

It should be taken into account that in our simulation exercise, only a portion of the complete egg-to-adult phase could be predicted, because our temperature records were limited to fourteen (summer) and seven days (winter). Longer temperature records, which would provide a more accurate picture of heat accumulation trends on differently oriented edges, might be necessary for the models to predict significant divergence in life-stage duration. Although most studies only use temperature to analyze and predict variations in insect life cycles as we have done here, other factors such as wind velocity, humidity, radiation, photoperiod or diet, can interact with each other in the field and crucially affect insect development (Rebaudo and Rabhi, 2018). Some of these factors and others such as behavioural thermoregulation and landscape topography are currently integrated into these models, affecting the predictions of the species responses to climate change (Barton and Terblanche, 2014; Barton et al., 2018; Bonebrake et al., 2014).

4.2. Final considerations

Our findings emphasize the need to consider geographical orientation and seasonal variations when studying edge effects on insect populations. Edge orientation can define microhabitats with different microclimatic conditions and determine habitat suitability for the growth of organisms. In the face of harsh climate at a regional scale, organisms could restrict their distributions to microhabitats with more favorable conditions which would, in this sense, constitute microrefuges that could allow them to survive (Bennie et al., 2008; Dobrowski, 2011). Our simulation exercise suggested that, at larger scales, increased temperatures could lead to more frequent pest outbreaks which could extend their distribution range to higher latitudes. All in all, our results suggest that locations in a fragmented forest, even differently orientated edges, are not equal in terms of the set of microclimatic conditions here studied. Subtle variations could influence organism fitness in different ways, which could affect species population dynamics, and for this reason, they should be considered in conservation programs of forest-living species.

5. Conclusion

This study provides additional evidence, using a large set of microclimatic variables, about differences in the abiotic edge effect in differently oriented edges, in summer and winter seasons. Furthermore, according to the simulation exercise, thermal variations like the ones here observed between microhabitats would have biological implications in the development speed of the leaf miner *L. huidobrensis* and its parasitoids. The environmental differences here observed at a small geographical scale, i.e. interior and differently oriented edges within forest fragments, could help us understand how species respond to the higher and more variable temperatures predicted by currently global climate change models. In this scenario, species could search for places with more favorable microclimatic conditions as shelter, to cope with harsh climate at large scales (Dobrowski, 2011). In fragmented landscapes, identifying microhabitats benefitting or harming insect populations is an important step to design management strategies towards pest control or natural enemy conservation in agricultural settings.

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